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Dead wood fungi in North America: an insight into research and conservation potential

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Abstract

Saproxylic fungi act as keystone species in forest ecosystems because they colonise and decompose dead wood, facilitating colonisation by later species. Here, we review the importance of intact forest ecosystems to dead wood fungi, as well as trends in their diversity research and challenges in conservation. Saproxylic communities are sensitive to transition from virgin forests to managed ecosystems, since the latter often results in reduced tree diversity and the removal of their natural habitat dead wood. The impact of dead wood management can be quite significant since many saproxylic fungi are host-specific. The significance of citizen science and educational programmes for saproxylic mycology is discussed with the emphasis on the North American region. We intend to raise the awareness of the role that dead wood fungi play in forest health in order to support development of corresponding conservational programmes.

Keywords

saproxylic fungi, dead wood, saproxylic biodiversity, coarse woody debris

Introduction

Dead wood is an essential component of any forest ecosystem. Its value for biodiversity and forest ecosystem function is hard to underestimate; dead wood protects soil against erosion, contributes to soil quality with massive organic and mineral inputs, improves water retention and creates multiple habitats for plants, animals and fungi (Stokland et al. 2012). Components of dead and decaying wood provide the energy necessary to

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facilitate the regeneration of trees in the form of carbon and nitrogen storages. In undisturbed and old-growth forests, dead wood exists in many forms, from entire standing or fallen trees to decomposing fragments of wood. These diverse woody elements co-exist across time and space. Dead wood is a challenging substrate to decompose. Enzymatic digestion of tough woody polymers such as lignin and cellulose is primarily performed by saproxylic fungi and bacteria, whose actions are complemented with additional mechanical disintegration by invertebrates (Keren and Diaci 2018). Saproxylic fungi thrive in temperate (Hodge and Peterken 1998; Purahong et al. 2018), as well as in other types of forest, facilitating cycling of nitrogen and other elements back to forest soils (Juutilainen et al. 2016). In addition, as pioneer decomposers, saproxylic fungi initialise ecological succession processes that sustains forest biodiversity, which makes them invaluable forest organisms. Numerous dead wood fungal species have been described with more being discovered regularly, but the knowledge about their diversity or species loss remains scarce (Hawksworth 1991; Runnel and Lohmus 2017). Importantly, some saproxylic fungal species have specific preferences for substrate types, such as coarse woody debris (CWD) or standing dry trees (Nordén et al. 2013).

Earlier research demonstrated that in North American forests, decomposing CWD could cover up to 25% of forest ground surface (Speight 1989), with dead wood making up a third of total woody biomass in most ancient forests. In a managed North American forest, dead wood content can be reduced by up to 15% from its original amount (Harmon 2001). This reduced proportion is a result of a combination of factors such as land management practices, forest type and climate change. Forests, especially in the circumboreal zone, are experiencing some of the largest global warming-induced temperature increases on earth, resulting in yearly tree loss due to increased exposure to insect infestations as well as more frequent wildfires (Balling et al. 1998; Hansen et al. 1996; Serreze et al. 2000; Soja et al. 2007).

To sustain human activity, forests continue to be cleared and the land is transformed to suit the immediate need (DeFries et al. 2004; Vitousek et al. 1986). Older trees are regularly removed for timber or to make room for agriculture or urban sprawl. However, as population needs and infrastructures evolve, unused croplands may transition back to forests. Nevertheless, most replanted forests are far too young (Tierney et al. 2017) and they lack the structural complexity needed to support diverse saproxylic organisms. In highly populated regions, any decomposing wood that could potentially accumulate is periodically removed for fuel, decorative purposes or when 'cleaning' the landscape (Fig. 1) (DeFries et al. 2004). In addition, logging is a common strategy in forest management to guard against the spread of species targeting decomposing wood (Karvemo et al. 2017). For example, bark beetles are natural inhabitants of old-growth trees and their control has started a debate between loggers and environmentalists who disagree on the best way to combat them (Grotta 2013; Stokstad 2017). Similar controversy dominates the discussion of use of controlled/prescribed burning for dead wood restoration (Eales et al. 2016).

The aforementioned factors have led to habitat loss and a sharp decline in species diversity amongst various taxa of all saproxylic organisms and especially fungi (Jonsson et al. 2005). The removal of dead wood has resulted in an incalculable extinction

Figure 1. Managed park with almost no dead wood. New Jersey, USA, 2018. Photo M. Shumskaya.

debt facing saproxylic taxa worldwide (Chen and Hui 2009; Hanski 2000). For example, out of 45 well studied saproxylic beetle species existing during the Bronze Age, less than 1/3 have avoided extinction and were considered rare 30 years ago (Speight 1989). The reduction in dead wood habitat lowers saproxylic species richness and decreases genetic diversity within populations, leading to rippling consequences for forest ecosystems specially adapted to vast saproxylic communities and leaving them vulnerable to disturbances and extinction (Sebek et al. 2013).

Most of ongoing conservational efforts aim to restore falling biodiversity of plants and animals via assigning spaces and/or species official designations, like endangered or threatened, accompanied by legal protection (Juutilainen et al. 2016). Unfortunately, logging of damaged or dead trees (salvage logging) in both North America and Europe is often conducted even in areas reserved for conservation and otherwise protected from logging, decreasing the biodiversity of saproxylic species (Thorn et al. 2018). Current forest management and conservation strategies are not sufficient to preserve saproxylic biodiversity, in particular fungi that are specialised to CWD (Abrego and Salcedo 2013; Küffer and Senn-Irlet 2005). Little is being done to protect saproxylic biodiversity in the face of habitat loss and other anthropogenic threats. However, there are recent initiatives of the IUCN (International Union for Conservation of Nature) such as the Global Fungal Red List Initiative (http://iucn.ekoo.se/iucn/about) or European Red List of Saproxylic Beetles (Nieto and Alexander 2010).

In this work, we intend to overview the current knowledge on the dead wood fungi biology, ongoing research and conservation with the emphasis on North America to promote public education, research and conservation programmes in saproxylic mycology in this region.

Dead wood fungi at a glance

Saproxylic fungal communities constantly transform as wood decomposes. The decomposition pathways vary greatly amongst the tree species, surrounding biotopes, the landscape matrix, forest history, spore rain and numerous other factors. This process depends highly upon the structure and composition of the saproxylic fungal community (Kubartová et al. 2015; van der Wal et al. 2015). Different types of saproxylic fungi demonstrate a gradient of enzymatic abilities and, traditionally, are classified according to the specific substrates they digest and the type of resulting rot. In general, white rot refers to fungi that can process lignin, brown rot fungi digest hemicellulose and soft rot fungi possess enzymes that break down cellulose (Rajala et al. 2015). As Boddy and collaborators (Boddy et al. 2007) demonstrated, wood-decaying fungi latently colonise living angiosperms and, after the trees are dead or damaged and water content in the sapwood is reduced, the fungi start to form fruit bodies.

Once started, decomposition gradually accelerates. Initially, when the wood is still very rigid, the heartwood is dominated by white-rot fungi; as fungi reproduce and develop, the number of brown-rot species increase heavily (Fig. 2) and the decomposition reaches its intermediate stage (Hiscox and Boddy 2017; Mäkinen et al. 2006) with fungi forming fruit bodies from early to late decay stages (Fig. 3). Finally, when wood is nearly completely broken down, the fungal fruiting bodies are no longer visible (Renvall 1995).

Figure 2. Brown rot of *Fomitopsis pinicola*, a common polypore on European spruce, *Picea abies*. Finland, Sipoo, Rörstrand, 2013. Photo D. Schigel.

Figure 3. Fungal fruit bodies are formed as wood decomposes and fungal species compete for resources and succeed each other. Bright annual fruit bodies of *Laetiporus sulphureus* on oak logs. Lithuania, Punios šilas, 2017. Photo D. Schigel.

Fungal hyphae absorb nutrients from degraded wood, then grow and expand until they reach and intertwine or penetrate roots from surrounding trees and plants. Mutualistic relationships between fungi and plants allow plant roots to use much of the absorbed minerals (Baldrian 2017), greatly expanding the surface area and absorption capabilities of the root system. In return, trees and plants provide heterotrophic fungi with carbohydrates and sugar (Bobiec et al. 2005). This absorption system, while sophisticated, is not 100% efficient, leaving excess nutrients to pool in the soil and mineralise, encouraging seedling recruitment. Nearly all the nutrients held in densely shaded soil are provided and replenished by fungal hyphae. Fungal mycelium also lends structural support to soil which slows the rate of erosion (Zhang et al. 2016). Few people, outside of specialised researchers, realise the link between the dead wood, soil quality and soil stability; without the continuous presence of saproxylic fungi and dead wood, soil quality diminishes (Hartmann et al. 2012), producing low quality vegetation as land becomes unsuitable to sustain seed recruitment and development.

Research on saproxylic fungi: challenges

Alternating life cycles and reproduction patterns of fungi render quantifying and collecting samples a challenging task as the detectability of different species greatly varies

within and across fungal taxa, with many species being cryptic (Halme and Kotiaho 2012; O'Brien et al. 2005). In order to get an inclusive picture of the local saproxylic fungal community, study sites must include all present tree species, need to be sampled repetitively, across a large spatial scale and over more than one growing season since fungal communities vary between decomposition stages which can continue through multiple decades (Saint-Germain et al. 2007). Until recently, few well-designed studies on saproxylic fungi were completed on a scale large enough to overcome these obstacles. Most of the research was being done on CWD (Grove and Forster 2011), with smaller diameter dead wood largely neglected in favour of larger samples housing more saproxylic organisms (Juutilainen et al. 2011) with some exceptions (Juutilainen et al. 2014). Regionally, studies of boreal forests overwhelmingly dominate in traditional dead wood conservation (Seibold et al. 2015), while tropical and subtropical forests, the greatest biodiversity hotspots on earth, remain vastly understudied (Dirzo and Raven 2003; Hansen et al. 2008).

Fortunately, the recent introduction of new sampling and molecular sequencing techniques and metagenomics (metabarcoding) as well as development of worldwide online DNA databases has greatly improved the research of cryptic dead wood fungal communities (Taylor et al. 2014). Metagenomics (metabarcoding) works with all of the genetic material from an environmental sample then analysing DNA sequences for all of the microorganisms present, using next-generation sequencing (NGS) techniques (Otlewska et al. 2014). The resulting sequences are compared against the reference libraries of Sanger sequences of well-identified specimens and thus multispecific metabarcoding samples are identified. This method allows collecting wood debris as samples in addition to fungal fruiting bodies to discover all cryptic or hidden species. Fruit body surveys combined with metabarcoding provide accurate, comprehensive data on saproxylic ecology (Ovaskainen et al. 2013).

With the use of molecular methods, we finally can start to understand the details of the dynamics of wood decomposition and the assembly processes of saproxylic fungi (Stokland et al. 2012). We now know that fungal micro-ecosystems are far more complex than once thought. Not only are there far more species of saproxylic fungi in existence than we thought, but the dynamics of succession and species assembly associated with dead wood decomposition are variable and adaptable and continues in the soil (Mäkipää et al. 2017). Researchers have even observed a pronounced preference for different tree species amongst saproxylic fungi that is comparable to, if not greater than, that of symbiotic and parasitic fungal taxa (Purahong et al. 2018). Metagenomics allows large-scale studies to be performed on dead wood to produce global data on saproxylic fungal biodiversity, essential to devise a working conservation strategy (Baldrian 2017; Telfer et al. 2015).

The use of DNA techniques in saproxylic ecology makes it an intriguing, complicated, multi-factor interdisciplinary field that incorporates the most current technologies. In spite of the global importance of dead wood, currently nearly all publications on saproxylic mycology come from Nordic countries and Canada, where forest research benefits from studies on complex interactions between fungi and other organ-

isms (Heilmann-Clausen et al. 2017; Mäkinen et al. 2006); dead wood as a study system is less popular in the United States.

A possible explanation for this imbalance in research reports is an enculturated social prejudice toward fungi. In the United States of America, fewer undergraduate students majoring in biology are choosing fundamental research careers, especially in mycology, when juxtaposed with more glamorous options like health and business professions (Sauermann and Roach 2012). The fact that so little is known about the importance and functionality of fungi exacerbates the problem and perpetuates the cycle. Fungi are often considered as pesky landscape invaders, or something purchased at the local supermarket instead of vital members of a global ecosystem. If more undergraduate students and the general public understood the central role played by saproxylic fungi in nutrient cycling processes of the world's largest carbon stores and the subtle beauty of saproxylic organisms, their research would likely garner more attention. The Nordic, British and Japanese admiration for dead wood and saproxylic organisms is yet to find its way into the North American academic tradition.

Research on saproxylic fungi: can citizen science help?

Citizen science is a research performed by laymen guided by a research professional. It has been shown to effectively support biodiversity and conservation studies (McKinley et al. 2017), hence research in biodiversity of fungi (saproxylic in particular) can especially benefit from involvement of citizen scientists. There is an ongoing effort across the mycology community to collect and organise data on all new and existing fungal species, whose number is estimated to be around 3 million (Funk et al. 2017; Hawksworth 1991; O'Brien et al. 2005; Tedersoo et al. 2014). Currently, not only research universities, but also undergraduate colleges as well as citizen scientists across the globe participate in this project. "Amateur scientists" collect observations, photographs and tissue samples for DNA analysis in an effort to establish an extensive and accurate database and participation in research becomes more and more popular in the US. Numerous informal interest groups and citizen science initiatives have sprouted on the Internet (North American Mycoflora www.mycoflora.org, Mushroom Observer http://mushroomobserver.org, Denmark's Mushroom Atlas http://www.svampeatlas.dk, https://svampe.databasen.org, Finnish Atlas of Fungi http://sieniatlas.fi and many others). Citizen science data is aggregated together with professionally collected data by thematic and national biodiversity portals; the central access point and search is provided by the Global Biodiversity Information Facility (GBIF). By October 2018, over 80% of the world's digital biodiversity data in GBIF have been comprised by human observation records (www.gbif.org).

Active development of citizen science in saproxylic mycology would not only contribute to fundamental research, but also help to raise the awareness on the role of dead wood and its inhabitants to support conservational efforts. While mushroom hunters commonly collect macrofungi, educational programmes can help to direct their at-

tention to dead wood species and research centres can support DNA-barcoding of the collected cryptic samples. A collaborative project on macrofungi, the North American Mycoflora, has already started in the US in 2017 to facilitate collaboration between professional mycologists and citizen scientists.

Saproxylic fungi conservation

In general, there is a limited conservation effort to address overall fungal biodiversity, especially when compared to other taxa; the Red List of threatened species from the International Union for Conservation of Nature includes only 56 threatened Fungi, while listing 68,054 Animalia and 25,452 Plantae. The Endangered Species Act in the United States of America is not any different, listing only 2 Fungi (lichens), while including 1,459 Animalia and 947 Plantae. Most of the countries in the world lack national Red Lists of fungi (Willis 2018). The low number of fungi on the Red Lists can be partially explained by a perception of many scientists that fungal species are problematic to assess due to their cryptic nature, high diversity and lack of taxonomic, distribution and ecological data (Mueller 2017). Insufficient representation of fungi in the IUCN lists limits conservation efforts, which are currently inadequately low to preserve the known biodiversity of 120,000 fungal species, with the various worldwide estimates of 1.5–3.8 million species (Blackwell 2011; Hawksworth 1991, 2001; Hawksworth and Luecking 2017; Tedersoo et al. 2014). The highest number of fungi was described in 2017 in Asia (35%), far ahead of North America (9.5%), reflecting the imbalance of taxonomic effort (Willis 2018). Since less than 8% of species are believed to have been identified (Hawksworth and Luecking 2017; Mueller and Schmit 2007) and more than 1,000 species are being described each year (Hawksworth 2001), it is imperative to evaluate techniques to assess the conservation status and protect fungi and specifically saproxylic fungi, their habitat and their associated species.

A common strategy to combat biodiversity loss due to urban development is setting aside areas of forested or re-forested land specifically to serve as nature and wildlife conservatories (Suominen et al. 2015). Saproxylic species, however, cannot be effectively protected using re-forestation methods. In re-forested areas, trees often lack diversity and are typically young, so they will not begin to decay in the near future, breaking the temporal continuum of dead wood for saproxylic organisms to inhabit. Even if decomposing wood still somehow manages to accumulate, current land management practices typically call for removal of woody debris and thus remain saproxylic biodiversity unfriendly. As human populations remove or alter forests, saproxylic fungal populations decline (Abrego et al. 2014; Caughley 1994; Komonen and Muller 2018; Mäkipää et al. 2017; Ovaskainen et al. 2017). Decreased tree diversity and corresponding dead wood leads to an unavoidable decline in saproxylic fungal diversity (Purahong et al. 2018), which would impact other species that

depend on fungi to soften dead wood before it can be inhabited. Setting aside truly unmanaged, untouched forested areas will help to preserve saproxylic diversity because the overwhelming majority of dead wood fungi are habitat and species specific (Bader et al. 1995).

Saproxylic fungi in unpopulated regions such as boreal and tropical forests are not commonly exposed to the same hazards stemming from development. However, they are not exempt from serious threats to their habitat such as climate change, pollution, agricultural chemical runoff and forestry practices. As species richness decreases latitudinally from tropical regions to arctic boreal regions, diversity of saproxylic fungi is affected correspondingly, with exceptions in ectomycorrhizal and ascomycete fungi (Juutilainen et al. 2016; Luo et al. 2014; Tedersoo et al. 2014).

The good news is that, with the recent innovations in fungal research and recognition of the vital role of fungi in ecosystems, the discipline of conservation mycology is able to emerge (May et al. 2018). In Chile, for example, an impressive promotional effort of The Fungi Foundation (Fundación Fungi) has led to the inclusion of fungi into Chile's General Environmental Framework Law in 2010 requiring a mandatory inventory of fungal species, with an obligation to develop fungal baseline studies established in 2013 (www.ffungi.org). As a result, Chilean fungi are now considered when evaluating projects that alter natural environments of Chile. In Australia, conservation mycology is strongly supported by citizen science initiatives in mapping and monitoring fungi (Irga et al. 2018). Dead wood, the habitat of saproxylic fungi, is an important subject of ecological and conservation biology research in Europe: The V European Congress of Conservation Biology in 2018 (https://conbio.org/mini-sites/eccb2018) had multiple discussions on dead wood conservation.

Support of the same magnitude can be expected in North America. A common social perception of fungi as "bad" and dead wood as an "unattractive" fire hazard that attracts pests and potentially deadly pathogens (Pastorella et al. 2016) can be improved with the proper educational programmes. Hopefully, as we start to better communicate the importance of fungi, dead wood and, specifically, saproxylic fungi to future scientists, public, broader conservation community, land managers and policy-makers, they will start to appreciate the complexity of a forest, a system much more intricate than several trees growing together in a park. Understanding of all fungi will ensure their significant inclusion in conservation actions and funding in the USA (Allen and Lendemer 2015). As of now, there is no chapter on saproxylic biology in a common school textbook, but education can be achieved through additional after-school programmes, amateur clubs for public, professional development for forest managers or special topic courses at colleges. As untouched, primeval forests (Fig. 4) are increasingly replaced by novel ecosystems, parks and reforested sites, these artificially maintained locations are quickly becoming the only places where humans interact with natural environment. The charm of the dead wood microhabitat can come through learning of the biodiversity value of the concealed worlds of hollow trees and decaying logs once they are left in parks by educated management (Fig. 5).

Figure 4. Fallen and standing dead wood are natural to primeval taiga. Russia, Altay, Balykcha, 2017. Photo D. Schigel.

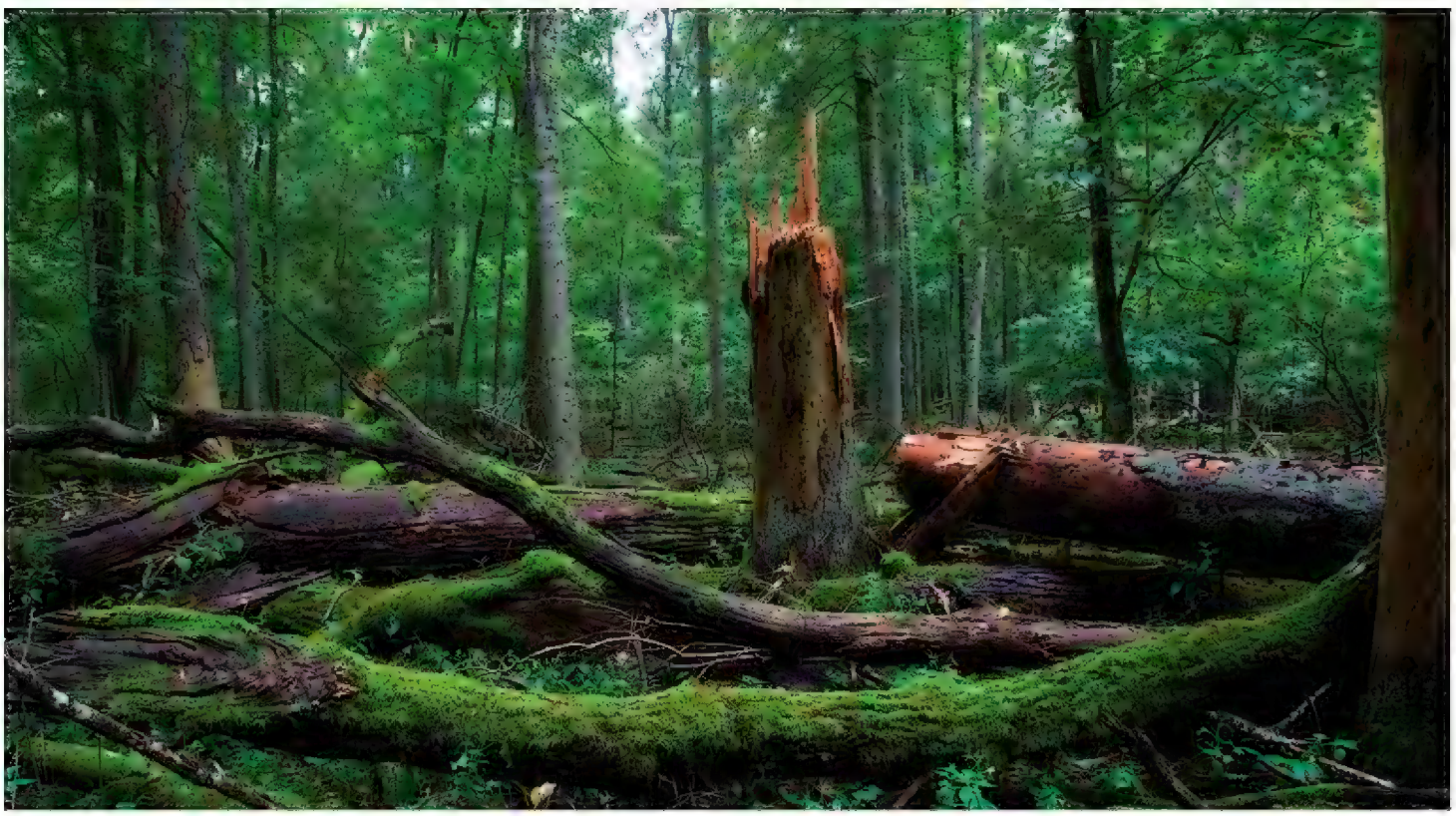

Figure 5. Wild and powerful beauty of undisturbed dead wood in a protected mixed forest. Lithuania, Punios šilas, 2017. Photo D. Schigel.

Conclusions

Saproxylic fungi play a vital role in forest ecosystems. Anthropogenic pressures like climate change, pollution, urban sprawl and agricultural runoff threaten the world's forest biomes, causing dramatic loss of habitat and resulting in rapid decline of biodiversity, including the nearly invisible biodiversity in dead wood. A decline in the global population of saproxylic fungi will have cascading and far-reaching negative consequences. It is vital to raise social awareness on saproxylic organisms and incorporating saproxylic fungi into ongoing and future restoration/conservation plans, especially in North America. Educational programmes should improve the overall attitude to dead wood as an essential forest component for both park management practices and public opinion. Changing the way society views dead wood and its fungi is an important step in attracting efforts to research and conservation of saproxylic biodiversity.

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